

## THE ROLE OF INHIBITORY STIMULI IN THE CHOICE OF OVIPOSITION SITE BY PHYTOPHAGOUS INSECTS

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The examination of substrate selection for oviposition behaviour by specialist phytophagous insects like *Acanthoscelides obtectus*, *Bruchus pisorum*, and *Pieris brassicae*, revealed that such processes were governed by information probably obtained through similar receptors to those taking part in feeding preference or rejection. The role of the ovipositor is assumed to be secondary or negligible. The receptors respond to a wide variety of inorganic or organic compounds of very dissimilar structure which inhibit oviposition on the most preferred host plants. Paradoxically, though females select the suitable oviposition media for the progeny, oviposition stimuli still do not reflect the quality of the substrates as larval food. Oviposition preference of the adults seems to be narrower than the range of substrates suitable for larval development.

Sign stimuli governing oviposition behaviour in phytophagous insects have been studied mostly from the point of view of host plant or substrate-specific stimuli (oviposition stimulants eliciting the egg-laying response.) Much less has been done to reveal the importance of *inhibitory* stimuli in determining the host plant range in oviposition site selection<sup>1)</sup>, or more generally, the possibility of inhibiting oviposition on the preferred substrate. This question is the more challenging since it could provide fundamental information for developing new selective pest control methods.

On the basis of experiments and observations on the egg-laying behaviour of phytophagous insects which are highly specialised in their selection of oviposition sites, Jermy (1965) proposed a two-way specialization of chemoreceptors governing oviposition. As with food selection by phytophagous insects, the inhibitory stimuli were regularly determinants, *i.e.*, the effect of the most potent stimuli or complex of stimuli inducing oviposition could be masked by inhibitory substances (antiovisitants) at an appropriate concentration. This assumption has been supported by the results of experiments carried out on various insect species indicating that egg-laying behaviour can be disturbed by the presence of various substances acting as contact chemical inhibitors (Gupta & Thorsteinson, 1960; Jermy, 1965; Terofal,

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<sup>1)</sup> The notion "oviposition site selection" is used here in a narrow sense, *i.e.*, it would not include orientation towards the substrate and refers only to the behavioural steps when contact has already been established between the insect and its oviposition substrate.

1965; Matsumoto & Thorsteinson, 1968; Mehta & Saxena, 1970; Cirio, 1971; Robert, 1971; Söme & Rygg, 1972; Fletcher & Watson, 1974; Lundgren, 1975; Muschinek *et al.*, 1976; Flint *et al.*, 1977; Rothschild & Schoonhoven, 1977).

Olfactory and/or contact chemoreceptors perceiving the presence of oviposition stimulants were mostly found on the head appendages and/or on the tarsi (Yamamoto & Fraenkel, 1960 a, b; David & Gardiner, 1962; Terofal, 1965; Yamamoto *et al.*, 1969; Benz, 1969; Yamada, 1970, 1971; Altwegg, 1971; Städler, 1974, 1977). However, very little is known about the role of chemoreceptors which may be located on the ovipositor of phytophagous insects.

In behavioural tests Féron (1962) and Sanders (1962) could not find any indication of chemoreception by the ovipositor of *Ceratitis capitata*. On the other hand, *Anastrepha suspensa* females could differentiate between agar domes impregnated with various chemicals and covered by a wax coating so that the only information the females could obtain about the internal characters of such oviposition substrates must have been obtained from chemoreceptors on the ovipositor (Szentesi *et al.*, *in litt.*).

In addition, the results of ablation experiments with *Acanthoscelides obtectus* led Szentesi (1976) to conclude that such receptors were present on the ovipositor. Rothschild & Schoonhoven (1977) assumed that some elements discouraging egg-laying in *Pieris brassicae* are perceived through the tip of the abdomen. Oviposition by locusts is at least partially guided by chemoreceptors on the ovipositor (Norris, 1968). Data on chemosensory discrimination by the ovipositor are more numerous for parasitic wasps (*e.g.* Ganesalingam, 1974).

As far as the authors are aware, no investigations have been undertaken to find out whether anti-ovipositants are perceived by specific deterrent receptors situated on the head appendages or legs and which are known to function in perceiving antifeedants (Schoonhoven, 1977).

Investigations reported in this paper aimed to throw some light on: the nature of the chemicals acting as anti-ovipositants, the role of natural anti-ovipositants in host plant specificity of egg-laying females, and the position of the receptors responding to them.

## MATERIAL AND METHODS

### *Tests with Acanthoscelides obtectus*

Adults originating from a laboratory culture, maintained on dry beans (*Phaseolus vulgaris*), were used in the tests 1—3 days after hatching.

In two-choice tests, Petri dishes 10 cm in diameter were divided into four equal sections by 7 mm high cardboard walls, fastened with melted paraffin. The two oviposition substrates<sup>1)</sup> to be tested were distributed in opposite quarters of the

<sup>1)</sup> "Oviposition substrate" here refers to beans, peas, soybean etc. or beans, pebbles and glass beads of the corresponding size coated by powders, solutions or suspensions taken up in a 2% wheat starch solution.

dish. Ten ♀♀ and 10 ♂♂ were put in each dish.

Multiple-choice tests were also used. In some, each substrate to be tested was put on the bottom of a glass vial (20 mm diam. and 50 mm high). Two series of vials were arranged in a circle in a larger glass jar (150 mm diam. and 180 mm high) covered with linen cloth. Each substance was presented twice, the positions of the vials were randomized, and they were separated from each other by about 5 mm preventing the weevils from creeping directly from one vial into a neighbouring one.

In a second series of multiple-choice tests, round dishes 14.5 cm diam. and 6.5 cm high, or 10 cm diam. and 2 cm high were divided by cardboard walls (7 mm high) into ten or eight sectors. One type of substrate was placed in each sector with the same types in opposite sectors.

Glass cover slides were treated on one side with either an anti-ovipositant compound or an oviposition stimulant (seed coat powder in 2% wheat starch solution) and then bound together so that treatments alternated. The slides were separated from each other by a gap of  $0.24 \pm 0.05$  mm and on top of the bundle was placed either a bean or a coating of oviposition stimulants to induce oviposition into the gaps containing the different media.

#### *Tests with seed coat materials*

Seed coats of dry beans and peas were removed, ground and then thoroughly mixed with each other or with wheat starch powder in varying proportions (Table II). Wheat starch powder was used as an indifferent additive to "dilute" or substitute seed coat powders in control treatments. The powders were stuck on the surface of glass beads with a 2% wheat starch solution following the method of Muschinek *et al.* (1976).

Separate tests with seed coat extracts were also performed. 1000–1500 g of whole seeds of dry beans or peas were washed with 150–200 ml distilled water or with n-hexane for 30 sec and the extracts were used to cover glass beads (6 mm diam.). Extract-coated vs. solvent-treated glass beads were presented in two-choice tests.

#### *Determination of suitability of seeds for larval development*

Twenty g of dry beans (*Phaseolus vulgaris*), garden pea (*Pisum sativum*) soybean (*Glycine max*), and cowpea (*Vigna sinensis*), respectively, were put in 200 ml plastic cups covered with dense linen cloth. One day old eggs of *A. obtectus* were placed on the seeds in each cup,  $171 \pm 43$  per cup. After the penetration of the larvae into the seeds, all the nonviable eggs and the egg-shells were removed and counted. Hatching adults were collected and recorded daily.

All tests were carried out in total darkness at 24° to 26° and 65–70% r.h. and terminated after 10 days. Eggs laid were counted. Usually five to ten replicates were used per test. Degree of preference (+) for or rejection (—) of a certain substrate was determined in two or multiple-choice tests by the so-called discrimination coefficient (David & van Harrewage, 1970). Comparisons of means

of such tests were carried out by using Duncan's new multiple-range test for equal or unequal sample sizes.

#### *Inhibition of oviposition by Bruchus pisorum on green pods*

Ten green pea pods immersed with their petioles in water-filled vials were sprayed with 2% Bordeaux mixture [ $\text{CaSO}_4 \cdot \text{Cu}(\text{OH})_2 \cdot 3\text{Ca}(\text{OH})_2$  complex]. The pods were arranged in a circle in a cylindrical glass jar alternately with ten untreated pods. Fifteen adults were introduced into the jar and the eggs laid on the pods were counted after 48 h.

#### *Inhibition of oviposition by Pieris brassicae by various compounds*

Laboratory-reared adults were used 4 days after emergence for the tests in a  $120 \times 52 \times 60$  cm size cage the walls of which were partly of glass, partly of nylon screen. Savoy cabbage leaves were cut to a standard size of  $57 \times 47$  mm and wilting was prevented by inserting the petioles in water-filled vials. The treated and control leaves were arranged in a random block using the whole of the bottom of the cage.

In other experiments with potted plants opposite leaves (two to four) were used, alternately treated, (sprayed or smeared with different chemicals) and untreated, (sprayed or smeared with distilled water and surfactant). The tests were carried out in a glass house under natural illumination and at fluctuating temperature. Peak oviposition periods were found to be at about noon. Numbers of egg-batches and eggs laid on the leaf-surfaces were counted and evaluated as signs of oviposition preference of adults. Artificial flowers containing honey-water served as food sources for the butterflies.

## RESULTS AND DISCUSSION

### *Acanthoscelides obtectus*

#### *Degree of oviposition preference and suitability of various leguminous seeds for larval development.*

In the field, females usually gnaw holes along the suture of the ripening bean pods and lay eggs into them. In stores, eggs are ordinarily laid under dry seeds. Just before egg-laying females examine beans thoroughly by palpation and this behavioural stage is especially intensive at the area of the caruncle.

In both dual choice and multiple choice experiments dry beans were preferred over all other species (Fig. 1a, b), but the other substrates were not wholly rejected and soybeans was generally next preferred. Without dry bean little discrimination occurred although peas were not favoured (Fig. 1c). Beans coated with 0.1M  $\text{CuSO}_4$  solution were strongly discriminated against (Fig. 1d).

The experiments showed that the acceptability of a given substrate was influenced substantially by the presence of alternative substrates. The acceptability of certain oviposition media may decrease in the presence of a preferred choice alternative, and increase greatly if there are only poor alternatives provided.

Several pea varieties proved suitable for larval development although mortality

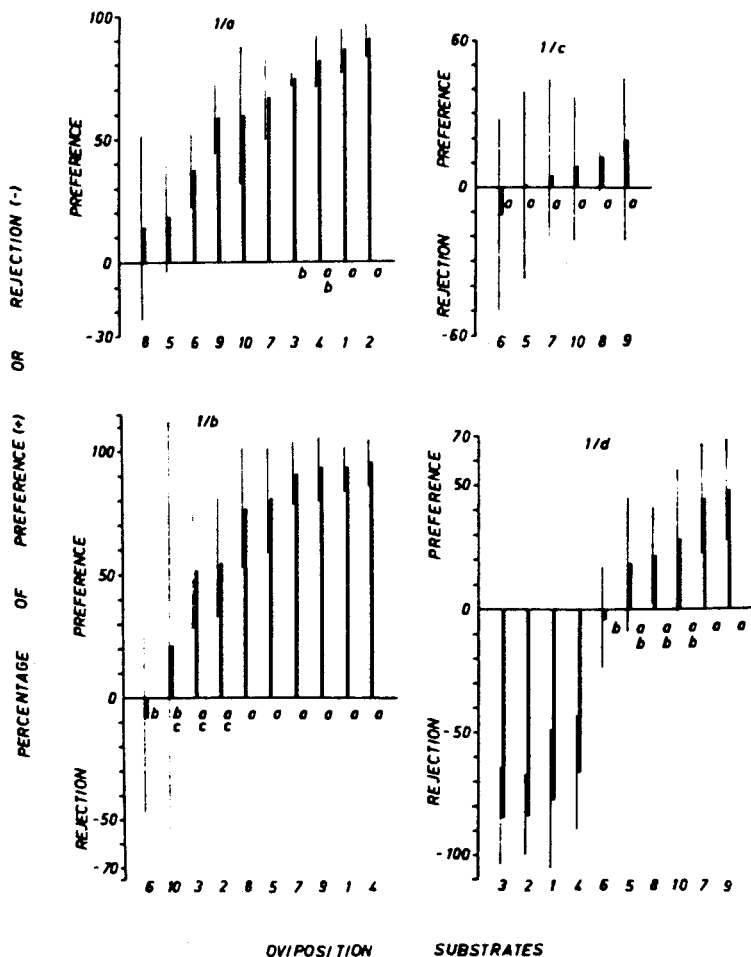


Fig. 1. Preference of ovipositing *Acanthoscelides obtectus* females for various host and non-host plants and substrates. a) two-choice test; b) multiple-choice test, substrates in vials; c) multiple-choice test, substrates in sectors, dry beans absent; d) multiple-choice test, substrates in sectors, dry beans treated with 0.1M  $\text{CuSO}_4$  present. Solid bars indicate mean discrimination coefficients, thin lines are standard deviations. In each set of data, means marked by same letters are not significantly different at 5% probability level (Duncan's new multiple-range test). — 1 = dry beans/pea — 2 = dry beans/soybean — 3 = dry beans/cowpea — 4 = dry beans/pebbles — 5 = soybean/pea — 6 = soybean/cowpea — 7 = soybean/pebbles — 8 = cowpea/pea — 9 = cowpea/pebbles — 10 = pea/pebbles.

was high compared with dry beans, and development time was substantially increased (Table I). The data show that oviposition preference as shown in Fig. 1 is not necessarily in accordance with the suitability of a seed as a larval food. The great difference between pea varieties is also remarkable since, compared with dry

TABLE I

*Suitability of leguminous seeds for the development of the larvae of Acanthoscelides obtectus*

Plant species and cultivars	%Mortality from L <sub>1</sub> to adults	Time in days necessary for development from L <sub>1</sub> to adults at 24°
<i>Phaseolus vulgaris</i>		
cv. Közép fehér	0.7	31—43
.. Korai vaj	4.1	31—54
.. Valja	8.2	31—47
.. Gépi arató	12.0	31—46
.. Budai piaci	13.0	31—46
<i>Glycine max</i>		
cv. ISz 10	100	—
.. ISz 14	100	—
.. GSz3	100	—
.. Ewans	100	—
.. Merit	100	—
.. Traverse	100	—
<i>Vigna sinensis</i>	100	—
<i>Pisum sativum</i>		
cv. Budai csemege	21.0	41—83
.. Grüne Perle	25.3	33—70
.. IP 4	27.4	34—82
.. IP 2	30.8	35—67
.. Kelvedon wonder	30.9	36—79
.. IP 3	49.1	38—77
.. Debreceni sötétzöld	63.2	43—70
.. Chrestensens Gloriosa	79.7	43—75
.. Express	80.4	46—77
.. IP 5	85.0	40—70
.. IP 7	88.5	49—82
.. IP 8	93.4	56—81
.. Iregi sárga	95.5	46—83
.. Bountiful	97.9	61—75
.. IP 6	99.1	60—65
.. Gloire de Quimper	99.2	56—63
.. Lincoln	99.4	77

beans, the non-preference was the same in all cases. Soybean and cowpea, the more preferred of the non-hosts for oviposition proved unsuitable as larval food (see also Basky, 1977).

These findings and other data (e.g. Basky, 1977) listing fifteen to eighteen plant species on which larval feeding has been observed, seem to support the view that adult oviposition range should be narrower than the number of plant species

allowing larval survival. See also Wiklund (1975) for detailed discussion of the same phenomenon in *Papilio machaon*.

*The cause of non-preference.* Non-preference for oviposition substrates can be caused by the lack of oviposition stimulants, by the presence of anti-ovipositants, or by both effects together.

Since in the choice tests pea was generally the least preferred seed, we assumed that an anti-ovipositant was present, which could be extracted and used to mask the stimulating effects of beans. Therefore, tests with seed coat extracts and with seed coat powders were carried out. The results show that the pea seed coat possessed both hexane- and water-soluble factors increasing the acceptability of glass beads compared with control beads, although the extracts were much less effective than those from dry beans (Table II). Pouzat (1976, 1977) has also proved the existence of ether-extractable stimulating factors in beans.

In a subsequent experiment carried out with seed coat powders evidence was gained that pea does not possess an anti-ovipositant for *A. obtectus* females (Table II). Even the mixing of nine parts of pea seed coat powder with one part of dry bean

TABLE II

*Oviposition preference of Acanthoscelides obtectus for host and non-host extracts and seed coat powders. Five replicates for each experiment.*

Treated (T)	Experiment	Untreated (U)	Discrimination coefficient (T/U% ± S.D.) <sup>3</sup>
<i>Extracts<sup>1</sup></i>			
a) Distilled water			
dry beans		water only	+ 55.5 ± 8.5a
peas		water only	+ 14.5 ± 11.8b
dry beans		peas	+ 57.2 ± 9.9a
b) n-hexane			
dry beans		n-hexane only	+ 23.6 ± 11.6b
peas		n-hexane only	+ 20.9 ± 15.0b
dry beans		peas	+ 33.6 ± 12.0b
<i>Seed coat powders<sup>2</sup></i>			
1 part bean + 9 parts-pea		1 part bean + 9 parts wheat starch	+ 54.4 ± 17.4A
1 part bean + 9 parts pea		wheat starch	+ 77.7 ± 5.0B
1 part bean + 9 parts wheat starch		wheat starch	+ 76.8 ± 4.4B
pea		wheat starch	+ 73.8 ± 18.3B

<sup>1</sup> 0.57–0.7 ml extract, equivalent to 7.26 g dry beans or peas applied on 40 glass beads.

<sup>2</sup> Dry beans and pea seed coat powder, or wheat starch mixed in various proportions to yield an average of 0.339 g subsequently taken up in 2% wheat starch solution and dried on 40 glass beads. After treatments an average of 0.097 g powder/40 glass beads (28.6%) did not stick on their surface.

<sup>3</sup> Means followed by same letters are not significantly different at 5% level. (Duncan's new multiple-range test.)

seed coat powder did not decrease oviposition preference for the latter substrate, and it is concluded that peas provide an indifferent substrate rather than being deterrent.

*Inhibition and stimulation of oviposition on dry beans.* Oviposition on dry beans can be inhibited or stimulated by inorganic and organic compounds (Tables III, IV). Copper sulfate exerted the strongest anti-ovipositant effect while other salts, such as NaCl, CuCl<sub>2</sub>, MnSO<sub>4</sub>, and MnCl<sub>2</sub>, inhibited egg-laying to various lesser degrees. MgSO<sub>4</sub> stimulated egg-laying, although it does not occur in dry beans in comparable amounts. MgSO<sub>4</sub> probably acts synergistically with unknown compounds of dry beans, since when it was applied to glass beads alone it did not stimulate. This result with MgSO<sub>4</sub> also shows that the oviposition stimulating effect is not restricted to specific secondary plant substances occurring in the host plant. Other Mg-compounds (MgCl<sub>2</sub>, MgO) did not show such effects.

Water-soluble copper compounds (CuSO<sub>4</sub>, CuCl<sub>2</sub>) exerted stronger inhibition than the insoluble CuO, although the difference was not proportional to the difference in solubility. Similar findings were reported by Britzkiy & Demkiv (1974) and Muschinek (1976) applying insoluble and chemically nondissociating inorganic

TABLE III

*Inhibition/stimulation of oviposition in Acanthoscelides obtectus by inorganic compounds*

Compound <sup>1</sup>	Replicates	Conc. (M)	Discrimination coefficient ± S.D.
CuSO <sub>4</sub> .5H <sub>2</sub> O	5	0.1	-81.7 ± 13.4
CuCl <sub>2</sub>	5	0.1	-42.5 ± 6.2
CuO	5	0.1	-18.9 ± 14.9
MgSO <sub>4</sub> .7H <sub>2</sub> O	25	0.1	+ 34.2 ± 14.2
MgCl <sub>2</sub>	10	0.1	-14.2 ± 10.7
MgO	5	0.1	+ 2.9 ± 24.2
MnSO <sub>4</sub>	5	0.1	-35.7 ± 10.2
MnCl <sub>2</sub>	5	0.1	-35.4 ± 18.7
K <sub>2</sub> SO <sub>4</sub>	6	0.1	+ 3.4 ± 21.8
KCl	10	0.1	-39.6 ± 15.3
Na <sub>2</sub> SO <sub>4</sub>	5	0.1	-23.8 ± 7.2
NaCl	7	0.1	-55.1 ± 11.1
H <sub>2</sub> SO <sub>4</sub> (pH = 1.62)	10	0.1	- 5.8 ± 18.2
H <sub>2</sub> SO <sub>4</sub> (pH = 5.46)	5	1.2 × 10 <sup>-5</sup>	-12.1 ± 11.1
HCl(pH = 5.9)	5	1.2 × 10 <sup>-6</sup>	+ 0.7 ± 22.9
KOH(pH = 12.4)	5	0.14	-17.8 ± 21.0
NaOH(pH = 12.3)	5	0.14	-27.2 ± 17.3

<sup>1</sup> One ml of each solution was dried on 40 g of dry beans. For suspensions 2% wheat starch solution was used as a carrier.



and organic copper compounds as feeding inhibitors.

The above results clearly show that substances of very different molecular structure can inhibit oviposition of the bean weevil on the most preferred substrate.

*Location of receptors responding to anti-ovipositors.* In tests with glass slides bound together with slits between, the numbers of eggs laid into the slits between the untreated (340 and 236 eggs) or oviposition-stimulant covered (167 eggs) slides did not differ significantly from those laid into the  $\text{CuSO}_4$ -treated slits (312 and 135 eggs). Thus, if the head appendages were able to perceive the normal stimulus-complex provided by the dry beans, the inhibitory stimuli, presumably perceived only by the ovipositor, did not influence egg-laying behaviour.

Szentesi (1976) found a tendency to prefer dry beans to other substrates even by females deprived of all head appendages and supposed a restricted role of the ovipositor in the choice of oviposition site. However, in view of the above results, it is conceivable that chemoreception by the ovipositor must, at most, play only a subordinate role in egg-laying behaviour. No electrophysiological or authentic SEM-morphological data on the ovipositor of the dry bean beetle are available.

#### *Inhibition of oviposition by Bruchus pisorum on green pea pods.*

In Central Europe *B. pisorum* is monophagous on *Pisum sativum*. When eggs laid on a pea pod were removed with a piece of the pod's epidermis and transferred to half-grown pods of *Lathyrus sativus*, the larvae developed normally in the seeds of the latter. Thus, host-plant selection of the pea weevil females is narrower than the range of plants suitable for larval development (Jermy, unpubl.). A non-protein amino acid oxalyldiaminopropionic acid isolated from *Lathyrus sativus* seeds (Rao *et al.*, 1964; Murti *et al.*, 1964) and known to be toxic for higher animals, apparently does not interfere with the development of pea weevil larvae after transfer.

The weevils laid an average of only  $0.1 \pm 0.32$  eggs on pea pods with Bordeaux

TABLE IV

*Inhibition/stimulation of oviposition in Acanthoscelides obtectus by organic compounds. Substrates prepared as in Table III*

Compound	Replicates	Conc.	Discrimination coefficient $\pm$ S.D.
Saccharose	2	0.1 M	-11.3 $\pm$ 2.6
L-Rhamnose	2	0.1 M	+ 1.9 $\pm$ 1.8
D-Raffinose	2	0.1 M	- 4.2 $\pm$ 22.2
2. 4. 6. trichlorophenoxy acetic acid <sup>1</sup>	4	1.0%	-93.1 $\pm$ 2.4
2. 3. 6. trichlorophenoxy ethanol <sup>1</sup>	4	1.0%	-98.8 $\pm$ 0.6
Quinine HCl	5	0.1 M	-10.0 $\pm$ 23.8
Strychnine sulfate	5	0.1 M	-55.0 $\pm$ 13.2
Digitonin	5	0.1 M	-48.4 $\pm$ 9.5

<sup>1</sup> 5ml 1% ethanol solution of the compounds dried on 100 g of beans.

mixture, compared with  $16.7 \pm 10.04$  eggs on the untreated ones. Thus, the copper complex almost totally inhibited oviposition.

#### *Inhibition of oviposition by Pieris brassicae.*

A wide variety of compounds produced various adverse effects on egg-laying behaviour by *P. brassicae* (Table V). These findings are in full accordance with those of Lundgren (1975) and Rothschild & Schoonhoven (1977). Both insoluble (Bordeaux or Burgundy mixtures, digitonin) and soluble (strychnine sulfate, quinine hydrochloride) inorganic and organic compounds showed significant inhibitory effects. Others, however, like isatin and rutin, did not hinder egg-laying on treated plants.

The fact that very different compounds may act as anti ovipositants supports the view of former authors (Terofal, 1965; Lundgren, 1975) that host plant specificity in the egg-laying female of *P. brassicae* is strongly determined by the botanical distribution of secondary plant substances inhibiting oviposition.

In order to find out the location of the chemoreceptors, savoy cabbage leaves treated with anti-ovipositants on the upper or on the lower surfaces were used as oviposition substrates together with control leaves.

When cut leaves were arranged so that their laminae stood in an angle of 40 to 50° to the ground, practically no eggs were laid on the treated leaves. This may be due to the fact that in such a position the females often sit on the lower surface

TABLE V

*Results of tests with anti-ovipositant compounds on the egg-laying of Pieris brassicae*

Compound	Replicates	Conc.	Treated Surface	No. of eggs on surface:			
				Treated		Untreated <sup>1</sup>	
				Upper	Lower	Upper	Lower
Bordeaux <sup>2</sup> mixture	4	1%	Upper	0	89	0	357
Bordeaux mixture	4	1%	Lower	0	372	0	538
Burgundy <sup>3</sup> mixture	4	1%	Upper	0	0	0	353
Burgundy mixture	4	1%	Lower	0	12	0	875
Strychnine sulfate	3	1%	Both	0	125	0	366
Isatin	3	1%	Both	0	63	0	36
Digitonin	3	1%	Both	0	0	0	439
Rutin	3	1%	Both	0	276	0	213
Quinine HCl	3	1%	Both	0	0	0	152
Genistein	3	1%	Both	0	374	0	580
Vincamin	3	1%	Both	0	744	0	618

<sup>1</sup> Surfactant, Tween 20 added to solutions or suspensions; also used as control treatment at concentration of 0.03—0.1%. —<sup>2</sup>CuSO<sub>4</sub> + Cu(OH)<sub>2</sub> —<sup>3</sup>CuSO<sub>4</sub> + Na<sub>2</sub>CO<sub>3</sub>.

during egg-laying. Thus they were discouraged by the anti-ovipositants both during the first contact with the upper surface, and during oviposition when sitting on the lower surface. When the leaves were horizontal, the females usually laid eggs by holding the forelegs on the upper surface and bending their abdomens to the lower surface of the leaf. In such an arrangement the leaves with anti-ovipositant-treated upper surfaces were definitely less preferred, while leaves treated on the lower surfaces were only sometimes less accepted than the control ones (Table V).

The results show that if there are separate deterrent receptors responding to anti-ovipositants they are most likely to be located on the legs where Terofal (1965) found receptors perceiving sinigrin.

### CONCLUSIONS

Oviposition by *A. obtectus*, *B. pisorum* and *P. brassicae*, which lay their eggs on a limited range of plant species can be inhibited even on the most preferred substrates by very different substances. This supports our former assumption (Jermy, 1965) that the effects of natural oviposition stimulants can be masked by anti-ovipositants of very dissimilar chemical structures. Thus it should be possible to find compounds capable of controlling insect pests with specialized egg-laying behaviour without polluting the environment.

The chemoreceptors presumably located on the ovipositors of the insects studied play only a subordinate role in governing egg-laying behaviour. Thus, the information on oviposition site selection is probably perceived by chemoreceptors located on other parts of the body such as the legs and head appendages.

The sensitivity to various substances with anti-ovipositant effects shows that species-specific plant substances inhibiting oviposition play a decisive role in determining the host plant range of egg-laying females. This type of sensitivity raises the question of the chemoreceptor mechanism involved since at present there is no explanation of the fact that substances of very different chemical and physical properties can evoke the same response at the behavioural and presumably also at the receptor level.

The presence of the host plant leads to rejection of other possible hosts or non-hosts as oviposition substrates even if they are more or less suitable for larval development. But in the absence of the host plant non-hosts, which are totally inadequate for larval development, may be preferred for oviposition. In these species at least, oviposition seems to be directed by stimuli appropriate only to the egg-laying process and without reference to the nutritive value of the substrate for the larva. Our findings also support the idea that adults lay eggs on fewer hosts than those which could serve as adequate food sources for larvae. This oviposition strategy is optimal because in choice situations, and if the host is present, the majority of eggs is laid on the latter. However, in the absence of the host plant, other oviposition substrates, normally not in the range of hosts, are also exploited to various extents on the basis of the more or less adequate oviposition stimulants which they provide.

Dry pea seeds do not possess any substance which inhibits egg-laying by bean weevil females. Nor do they seem to contain special oviposition stimulants, although peas are much more acceptable than pebbles or glass beads. Therefore, it is considered to be an indifferent oviposition substrate the value of which for oviposition is always relative to the alternative choice present. By contrast, pea seeds do possess inhibitory chemicals for larval development and there are substantial differences among pea varieties in this report.

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#### RÉSUMÉ

#### RÔLE DES STIMULI INHIBITEURS DANS LE CHOIX DU LIEU DE PONTE CHEZ LES INSECTES PHYTOPHAGES

On a fait des essais avec *Acanthoscelides obiectus*, *Bruchus pisorum* et *Pieris brassicae*. La non-préférence pour des substrats de ponte peut être due à l'absence de stimulants de ponte, à la présence d'"antiovipositants" ou à la combinaison de ces deux facteurs. Des types de composés très différents agissent comme "antiovipositants", et la spécificité de la plante-hôte est vraisemblablement déterminée par la distribution botanique des substances végétales secondaires. Les chimiorécepteurs des ovipositeurs des insectes étudiés ne jouent qu'un rôle subalterne dans la détermination du comportement de ponte. Les récepteurs situés sur les pattes ou sur les appendices de la tête sont probablement plus importants. Les adultes ne pondent pas leurs oeufs sur toutes les plantes qui pourraient offrir aux larves une alimentation adéquate.

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